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HARVESTER ANT WORKERS: VARIATION IN INVESTMENT OF SUBTERRANEAN TASKS

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HARVESTER ANT WORKERS:
VARIATION IN INVESTMENT OF SUBTERRANEAN TASKS

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A capstone project submitted for Graduation with University Honors

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Abstract

Harvester ants play a significant role as ecosystem engineers, influencing soil structure through nest excavation. Like other social insects, they cooperate through task allocation to efficiently accomplish things like nest excavation as a colony. Their nests are crucial to their survival; however, we do not know much about this topic since it often occurs underground. We explored how colony size influences nest architecture and task allocation of *Pogonomyrmex rugosus* harvester ants.

In this study, we divided 18 colonies into three size groups (100, 60, and 20 worker ants). Next, we painted 10 ants per box and observed their behaviors during the same time interval for five consecutive days. We took pictures every day to record the nest excavation progress. All results have shown a wide variation in worker behavior. We did not observe a typical routine; workers instead transitioned from one task to another. Based on the data collected, colonies with 60 and 100 worker ants had similar nest areas and complexity outcomes. However, the 60 ant colonies dug the deepest nests.

We found that the proportion of individual effort changed throughout the five days of the trial. We also found that the treatment we applied, which was splitting workers into three different colony fragment sizes, significantly affected the nest depth and area but not the nest complexity. Lastly, we found that the smallest colony fragments reach the same nest size no matter how many active excavators there are. However, in the colonies with 100 workers, nest building relies on how many excavators dig. These results suggest that individual behavior affects nest architecture which provides a basis for future research.

Acknowledgments

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Introduction

Most social insect colonies tend to allocate their tasks in order to get the job done more efficiently.^[1] Task allocation is an organizational process in which work is distributed among different workers. Individuals within a colony often collaborate to achieve common goals. The allocation of tasks among individuals is an imperative mechanism to ensure the success of those collective endeavors. This behavior is seen in bees. Individual bee workers vary in their choice of which tasks to perform as well as their persistence in performing such tasks.^[2] Other social insects such as ants are also known to allocate tasks among workers. Ants are well known for their remarkable abilities to organize themselves. However, scientists are still uncertain about how individual workers decide to organize their work to perform different tasks and how these decisions are made socially. Understanding the cognitive basis of task allocation in social insects may yield new insights into how cognitive processes operate in complex environments. Previous research has shown that *Formica* ant workers of different sizes specialize in different tasks.^[3] West and Purcell found extremely high task fidelity, wherein 98.6% of workers carried out the same task from one day to another.^[3] It has also been shown that there is a positive relationship between colony size and division of labor in *Pogonomyrmex californicus*.^[4] Colony size also affects interactions among individuals which in turn affects their task allocation outside of the nest.^[5]

Nest building is a major task that ants perform using task allocation. Their collaborative efforts to build the nest lead to nest architecture. Ants are well-known for their ingenious nest architecture. Nest architecture factors like depth and area are important factors in the dynamics of ant societies. In this project, we use Harvester ants which form colonies with overlapping nests, in which each individual ant performs multiple tasks. These factors impact the division of labor within the colony and hence the strategies used by those ants to defend against predation,

store food, and communicate. Harvester ants build robust nests but their digging patterns are rarely studied because nests occur below ground. It's for this reason that casting subterranean nests with aluminum has become important. In addition to the fact that it's interesting, casting nests also allows us to visualize the nest structure of different species.^[6] Due to this process, we now know that one species of Harvester ants (*Pogonomyrmex badius*) build complex nests with many chambers that can be up to 50 cm deep.^[6] A recent article shows that nest architecture is more affected by intrinsic factors rather than extrinsic factors.^[7] Intrinsic factors could include genes, interactions, or colony size. It has also been shown that nest architecture has an impact on the collective behavior of harvester ants.^[8] Beneficial nest architectures have a good network of connected chambers allowing the workers to move around faster.^[8]

While previous studies have identified how the nest structure affects ant behavior, we haven't looked yet at how individual behavior affects nest architecture. Our goal here was to bring these two areas together into one research project to study how individual behavior and task allocation affect nest architecture. Our aims for this project are as follows:

- (i) Determine if individual ants have assigned tasks. We want to look for consistency of behavior or task fidelity. Would the number of individuals carrying out an essential task like nest building going to be the same across the different treatments, or will the ants modulate their behavior so that a similar proportion of workers carry out the task? If it's the same number of individuals we would expect similar outcomes in nest structure. However, if it's a proportion of individuals, then we would expect the nest size to be proportional to the colony size.
- (ii) Discover how colony size affects nest architecture (depth, area, and complexity).
- (iii) Test whether the number of excavators influences nest development. We predict that more excavators will lead to larger and more complex nests than fewer excavators.

Methods

We worked with *Pogonomyrmex rugosus* (Rough Harvester Ants). Harvester ants are one of the most common ants in North America, and they are usually seen harvesting food from flowers or trees. The harvester ant colony is a remarkable system that involves incredible teamwork and communication. Harvester ants have a significant role in the community structure and ecosystem.^[9] Their removal and consumption of seeds heavily influence the species of plants existing around their nests. This means that with larger colonies, there is a heightened need for food. However, it doesn't negatively impact the environment because harvester ants are known to be ecosystem engineers. Their nest-building patterns influence soil structure and fertility, as well as their foraging, which helps increase plant diversity and richness.^[10]

Over a period of 10 weeks (3 trials, 5 days each), we collected worker ants to assemble 18 lab colonies. 13 lab colonies were collected from 4 field colonies at Islander Park (33.98°N, -117.31°W), and 5 lab colonies were collected from 2 field colonies from Sycamore Canyon Wilderness Park (33.96°N, -117.32°W) in Riverside, CA during June-August of 2021. Ants were collected from around their nest entrance. Ant collections were done 2-3 hours prior to putting them in the observation boxes. In the meanwhile, we maintained the ants in (10 x 15 x 20 cm) plastic containers side-lined with Fluon (a solution to make the side slippery so ants can't escape) and provided them with 2 pieces of cotton with water and sugar water.

Observation of individual behavior

We collected 180 individual workers for each lab colony (3240 total ants for this project).

Workers were distributed into groups of 100, 60, and 20 individuals. First, we placed ants in a refrigerator for 5 minutes. This step was critical because it allowed the ants to sleep so they wouldn't move around. We then painted the abdomen of 10 ants per group. In the 100 workers group, 10% of workers were painted, in the 60 workers group 17% of workers were painted, and

in the 20 workers group, 50% of workers were painted. We did this so we could repeatedly quantify individual behavior. We painted each of the 10 ants a different color. We used Testors® enamel paint and applied it with a toothpick on the ants' abdomen. On the days we took observations, we scanned to find each painted ant and recorded a snapshot of its behavior. We initially tried to use commercially available soil in the pre-trial phase of the experiment but we observed that ants were reluctant to dig. In subsequent trials, we collected soil from areas adjacent to the field nests and used it instead.

To begin observations, we filled transparent nest boxes (45.72 x 50.81 x 13.81 cm) with the collected soil in a laboratory setting (Fig. 2). In the laboratory, we had 18 of the transparent nest boxes which allowed us to observe 6 lab colonies per trial (since each colony takes up three boxes for the three different colony fragments 100,60, and 20). We provided each box with two microtubules filled with water and sugar water, respectively, and secured the liquid with cotton to serve as their food source. To feed, the ants bit the cotton piece to release the water. Later, we put each group in their respective boxes and took note of the colony and box numbers.

Table 1- Demonstrates how we kept track of how colonies were separated. In the lab we had 20 transparent boxes for observation, the box column is used to record which lab colony was kept in which box.

Location	Date Collected	Field Colony ID	Lab Colony	Box	Fragment Size
Islander	7/14/2021	1	1	20	100
Islander	7/14/2021	1	1	19	60
Islander	7/14/2021	1	1	8	20
Islander	7/14/2021	1	2	13	100
Islander	7/14/2021	1	2	16	60
Islander	7/14/2021	1	2	5	20

Location	Date Collected	Field Colony ID	Lab Colony	Box	Fragment Size
Islander	7/14/2021	1	3	4	100
Islander	7/14/2021	1	3	2	60
Islander	7/14/2021	1	3	7	20
Islander	7/14/2021	2	4	10	100
Islander	7/14/2021	2	4	15	60
Islander	7/14/2021	2	4	1	20
Islander	7/14/2021	2	5	12	100
Islander	7/14/2021	2	5	9	60
Islander	7/14/2021	2	5	14	20
Islander	7/14/2021	2	6	3	100
Islander	7/14/2021	2	6	17	60
Islander	7/14/2021	2	6	11	20
Sycamore	7/27/2021	3	7	3	100
Sycamore	7/27/2021	3	7	2	60
Sycamore	7/27/2021	3	7	1	20
Sycamore	7/27/2021	3	8	6	100
Sycamore	7/27/2021	3	8	5	60
Sycamore	7/27/2021	3	8	4	20
Sycamore	7/27/2021	3	9	9	100
Sycamore	7/27/2021	3	9	8	60
Sycamore	7/27/2021	3	9	7	20
Islander	7/27/2021	4	10	13	100
Islander	7/27/2021	4	10	10	60
Islander	7/27/2021	4	10	12	20
Islander	7/27/2021	4	11	16	100

Location	Date Collected	Field Colony ID	Lab Colony	Box	Fragment Size
Islander	7/27/2021	4	11	15	60
Islander	7/27/2021	4	11	14	20
Islander	7/27/2021	4	12	20	100
Islander	7/27/2021	4	12	19	60
Islander	7/27/2021	4	12	18	20
Islander	8/9/2021	5	13	3	100
Islander	8/9/2021	5	13	2	60
Islander	8/9/2021	5	13	1	20
Islander	8/9/2021	5	14	6	100
Islander	8/9/2021	5	14	5	60
Islander	8/9/2021	5	14	4	20
Islander	8/9/2021	5	15	9	100
Islander	8/9/2021	5	15	8	60
Islander	8/9/2021	5	15	7	20
Islander	8/9/2021	5	16	12	100
Islander	8/9/2021	5	16	11	60
Islander	8/9/2021	5	16	10	20
Sycamore	8/9/2021	6	17	16	100
Sycamore	8/9/2021	6	17	14	60
Sycamore	8/9/2021	6	17	13	20
Sycamore	8/9/2021	6	18	20	100
Sycamore	8/9/2021	6	18	19	60
Sycamore	8/9/2021	6	18	18	20

We observed the behavior change and switching of tasks of the ants that we painted over 5 consecutive days during the same time interval, 10:00 am-12:30 pm. Additionally, we observed the number of ants on the surface versus in the tunnels. We recorded the ants' behavior, to show whether the ants had task fidelity and to quantify individual effort in nest construction. In the end, when we have collected all observations, we created a pivot table with all the information on what each individual painted ant did all five days. We then manually noted whether it was an excavator. We also marked how many times it switched tasks instead of performing the same task (fidelity). In addition, we tracked how frequently it switched from one task to another. This was done to determine if ants switched between specific tasks more often than others.

Table 2- The behaviors that were recorded and a description of what was observed for each.

Behavior	Description
Excavating	Digging or moving soil from the tunnels to the surface
Removing cadavers	Moving dead bodies to the side of the box
Escaping	Climbing on sides of the box to try to get out
Surface activities	Drinking water/sugar water
Interacting	Two or more ants gathered and communicate
Inactive	Doing nothing or sleeping
Self-grooming	Cleaning themselves from soil

Nest architecture

Lastly, we took two pictures per box (front and back) at the end of each day to record the nest excavation progress. We also used those pictures to evaluate the nest architecture by calculating the depth, area, and complexity of each nest. (Fig. 1).

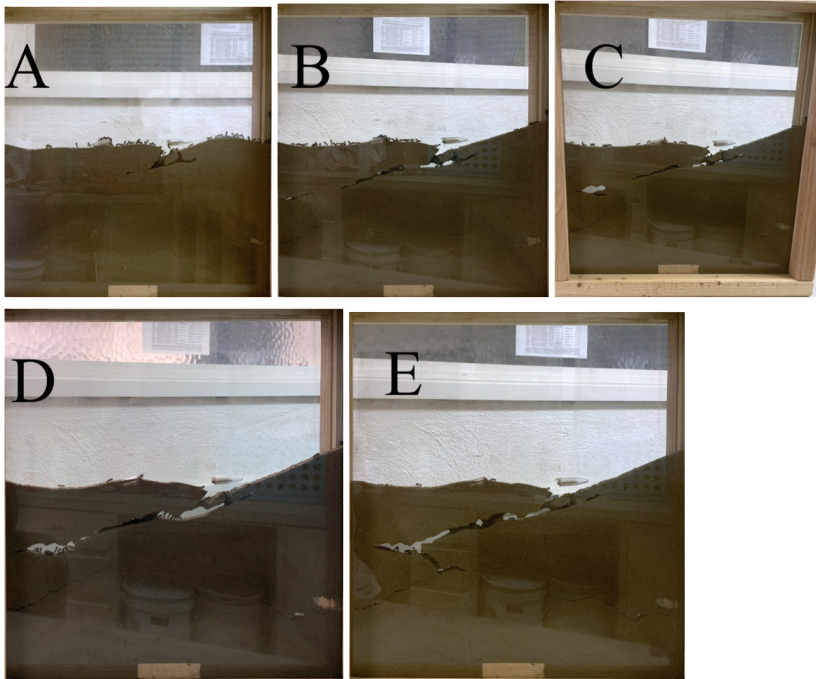


Figure 1 Shows the recorded nest-building progress throughout the five days of trial (A-E) for Lab Colony [13] Box [2] which had 60 worker ants.



Figure 2 Demonstrates the laboratory setup of the boxes where the nest building took place.

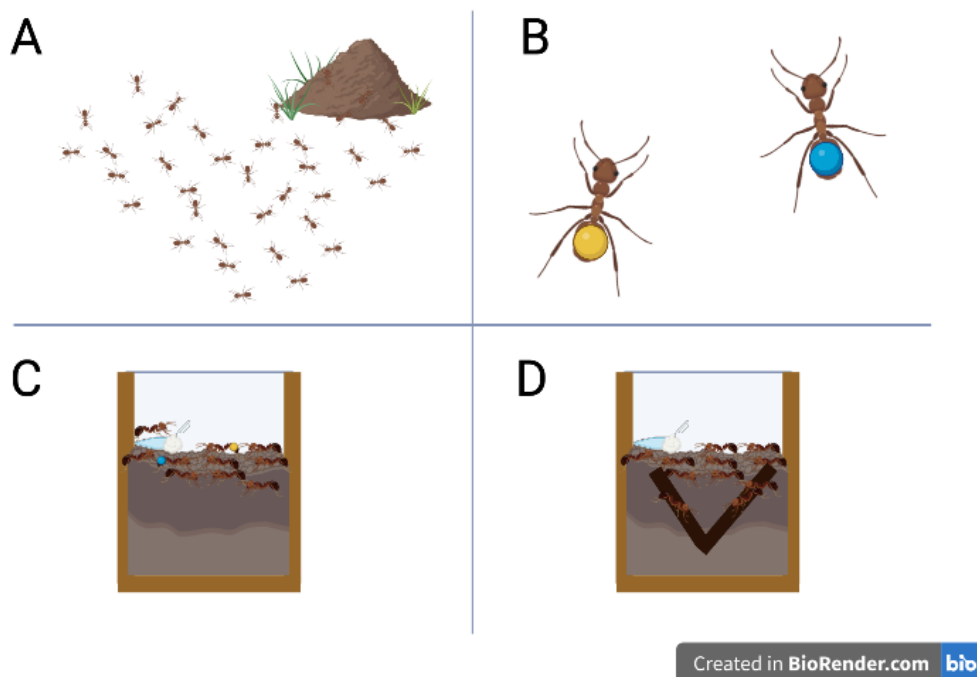


Figure 3 A visualization of the project methodology.
 (A) Field collection (B) Shows the process of painting the ants.
 (C) Behavioral observations (D) Taking pictures of the built nests.

Statistical data analysis

We used Google Sheets to organize the data collected and produce figures (5, and 7-12). Figure (3) was produced on the BioRender website and figures (4 and 6) were produced on the RAWGraphs website. <https://www.rawgraphs.io> We used ImageJ to calculate the nest depth and area for each box. We calculated depth by taking the average depth shown on both sides of the box, and the area by taking the sum of both sides' area. We performed a chi-squared test using the Social Science Statistics website <https://www.socscistatistics.com>, to calculate 1. If the proportion of individual effort significantly changed in the five days, 2. If there's a significant difference in switching tasks between excavators and non-excavators, and 3. If the proportion of excavators changed across the three treatments. We also performed three Anova tests using the Social Science Statistics website, to calculate whether a significant relationship exists between the applied treatments and the nest depth, area, and complexity.

Results

We first focused on the data from the observed individual ants to quantify the task allocation/fidelity of each. Then, we looked at the nest architecture and how the measures of depth, area, and complexity varied across all three groups. The nest measurements we used to get these results were from the pictures we took on the very last day of each trial (Day 5). At the end, we looked at whether the number of excavators in a colony has an impact on the final dug nest area.

Individual task allocation and fidelity

On the individual level we looked at the individual ant behavior and how that changes from day to day. We also looked at how it is affected by the number of workers per group.

Individual workers exhibited a range of behaviors during our experiment (Fig. 4). A chi-squared test revealed that the proportion of effort changed throughout the five days of trial ($\chi^2 = 15.98$, $p = 0.003$; Fig. 5).

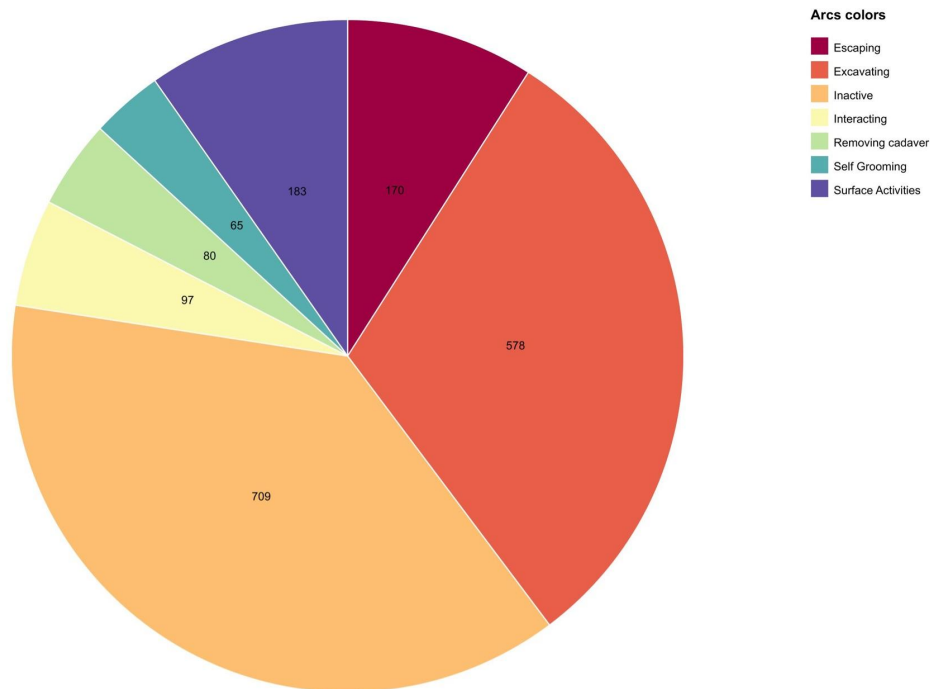


Figure 4 A pie chart of the frequency of the observed tasks. As shown, excavating is the most frequent active task which indicates that the worker ants spent most of their time building nests.

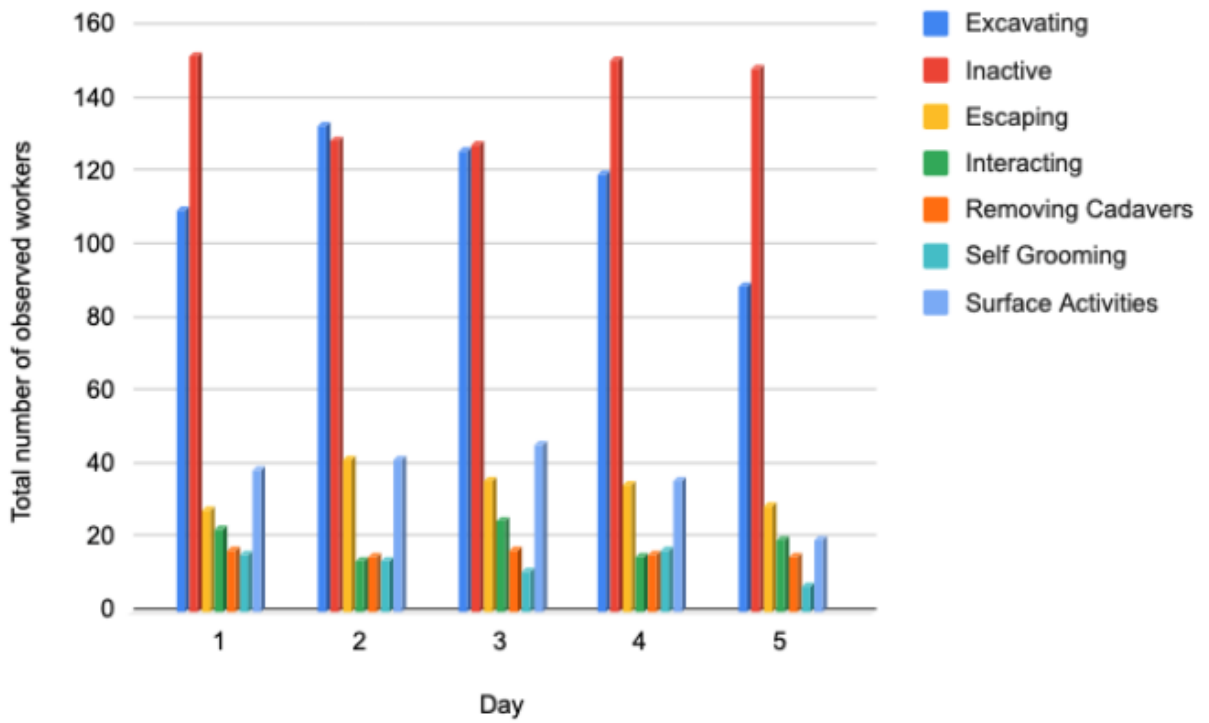


Figure 5 Presents the frequency at which each of the tasks was observed over the course of the five days of the experiment.

After that, we looked at task fidelity. We observed how often a worker ant maintained the same task and quantified task switching (Fig. 6; Table 3).



Figure 6 Represents how many ants switched from a certain task to another. The thickness of each line signifies how often each switch occurred. It also shows the rate of task fidelity represented by the parabolic shapes in the figure.

Table 3- Quantifies the number of times worker ants switched from one specific task to another over the course of the five days of trial.

Task 2 Task 1	Excavating	Removing Cadavers	Escaping	Surface Activities	Interacting	Inactive	Self- grooming
Excavating	202	18	37	45	22	147	11
Removing Cadavers	18	9	3	8	6	15	4
Escaping	46	6	19	12	6	42	4
Surface Activities	53	4	15	30	3	46	4
Interacting	21	0	6	4	7	34	2
Inactive	110	22	55	42	26	250	15
Self-groom ing	21	3	5	5	3	16	4

We kept track of how many times each ant switched tasks. Ants with (0) switches kept doing the same task every time they were observed over the course of five days, (1) switch means they switched tasks only once, and so on. We also recorded if those ants were excavators or not (Fig. 7), workers were counted as excavators if they were observed excavating at least once. A chi-squared test revealed that there isn't a significant difference between excavators and non-excavators when switching tasks ($\chi^2 = 8.85$, $p = 0.065$).

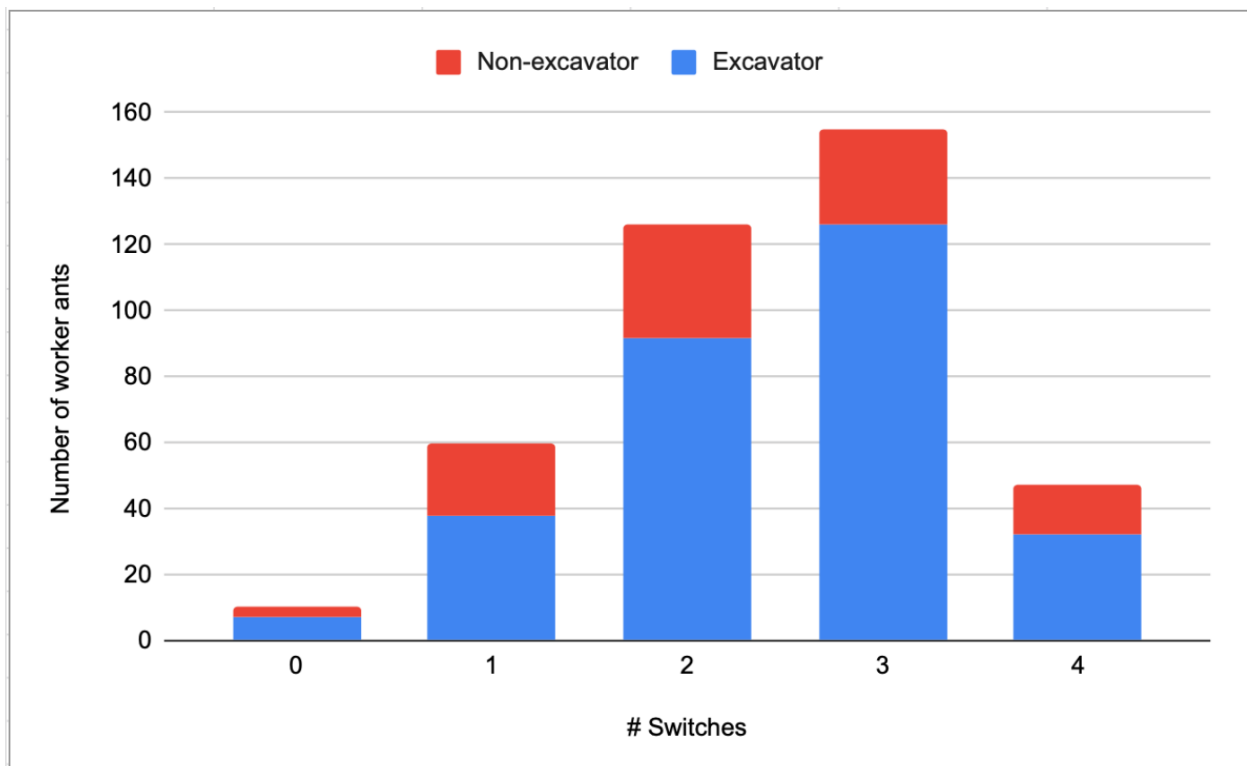


Figure 7 Demonstrates how many times worker ants switched from one task to another (0-4, high to low task fidelity). It also shows how many of these ants were excavators, which helped show that excavators are more likely to switch between tasks.

After that, we looked at how the different treatments of 20, 60, and 100 ants affected the proportion of active excavators in the five days of trial (Fig. 8). A chi-squared test revealed that the proportion of excavators was the same across the three treatments ($\chi^2 = 5.63$, $p = 0.23$).

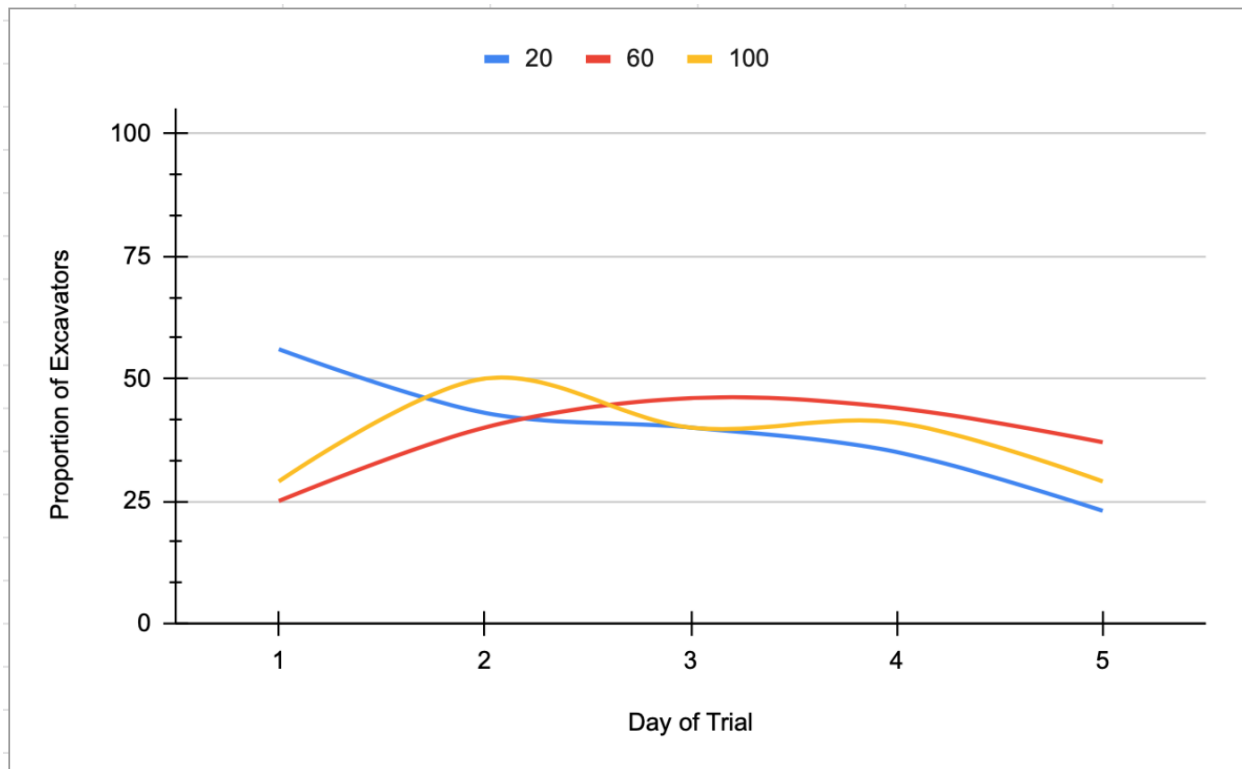


Figure 8 shows the proportion of excavators throughout the five days of trial in the three treatments. As shown, the proportion of excavators is the same.

How different colony sizes affect nest architecture

On the group level, we focused on how the number of ants per group affected the nest depth and area. We first looked at the sum of the area of nests that each of the colony fragments in the lab dug (Fig. 9). An ANOVA revealed that there is a significant correlation between the area of the nest and colony size. ($F_{2,51} = 6.70$, $p = 0.003$)

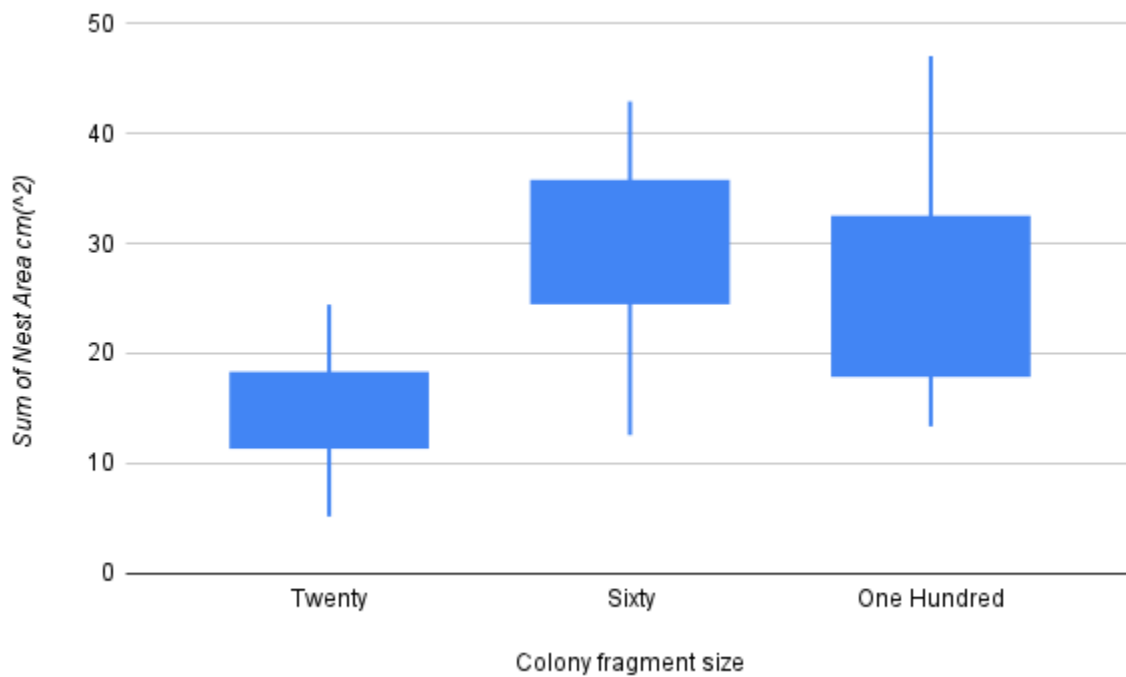


Figure 9 Comparison of the nest area between the three treatments. The figure shows that there is an association between colony size and the area of the nest they build.

Next, we looked at nest depth across the three treatments (Fig. 10). An ANOVA revealed that there is a significant correlation between the colony fragment size and the nest depth. ($F_{2,89} = 9.01, p = 0.0003$)

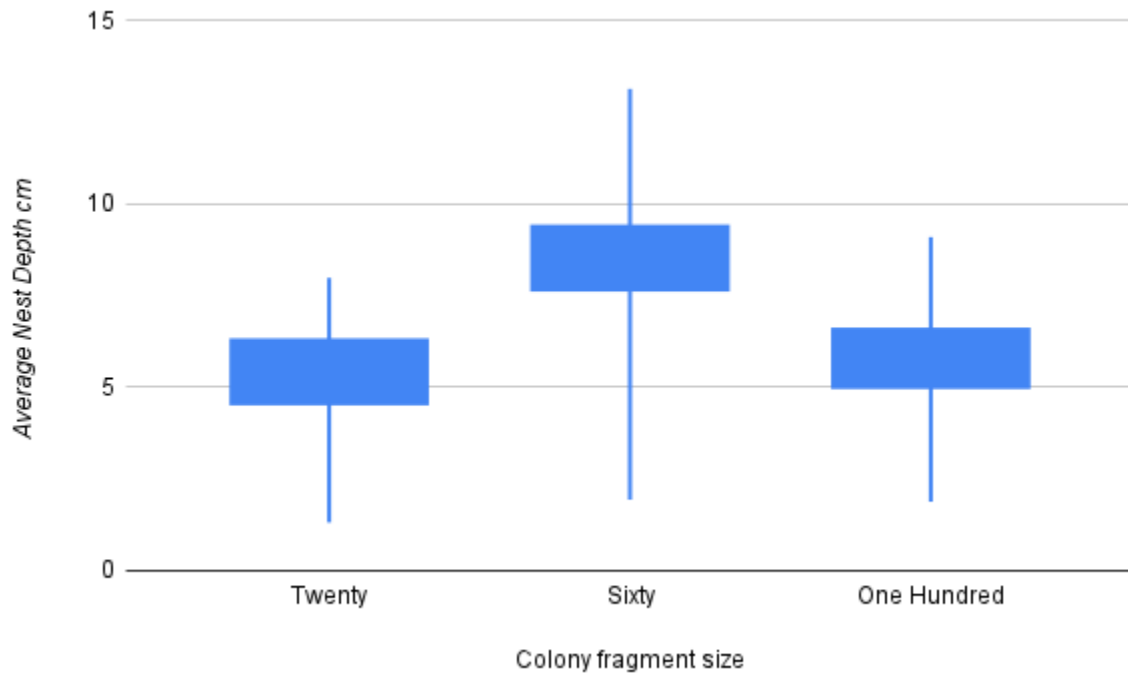


Figure 10 Comparison of average nest depth across the three colony fragment sizes. The figure shows similar outcomes from the 20, and 100 ant colonies while the 60 ants colonies seemed to dig the deepest nests.

Last we looked at nest complexity. We counted the number of tunnels per box to represent the complexity of a nest that the ants dug (Fig. 11). An ANOVA revealed that there isn't a significant relationship between the treatment and how complex the nest is ($F_{2,51} = 1.54, p = 0.22$).

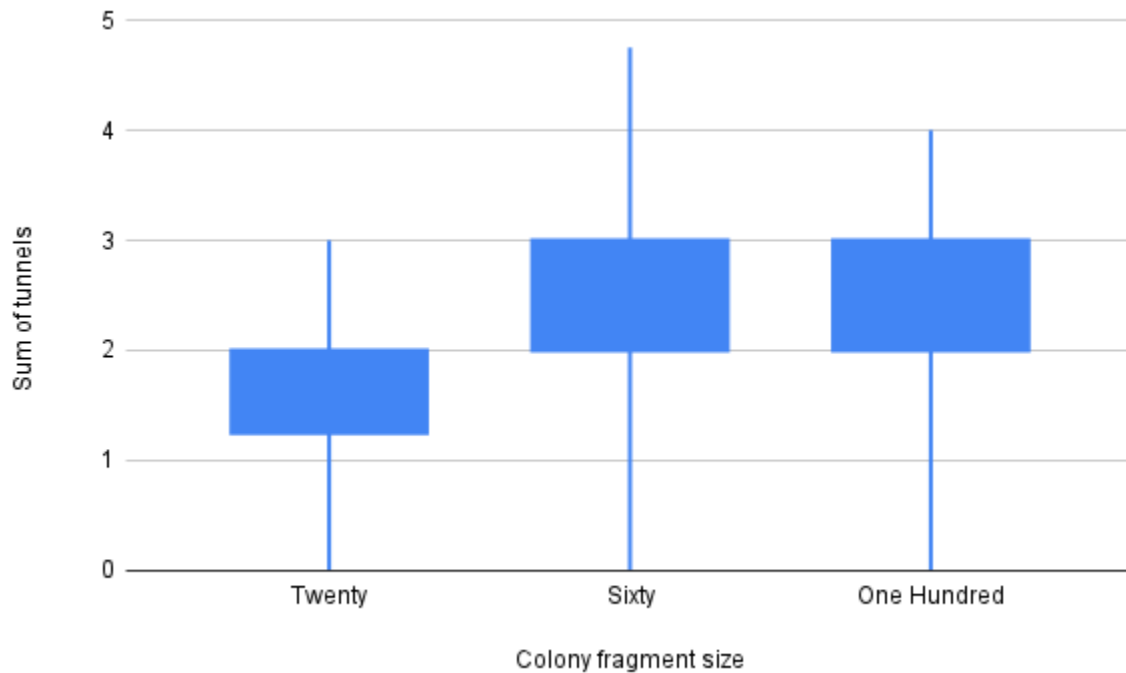


Figure 11 Comparison of nest complexity across all three colony fragment sizes. The complexity here was measured by counting the number of tunnels per nest. The 60 and 100 ant colonies were similar in complexity while the 20 ant colonies were far less complex.

Do individual behavior shape group outcomes

In the end, we looked at how individual behaviors affected the group outcome.

We saw that all three variables (area, depth, and complexity) follow the same pattern. We chose to focus on the area because we thought it was most likely to be strongly correlated with the number of individual excavators. We looked at the nest area vs the number of excavators (Fig. 12). We see that in the 20 worker fragments, no matter how many excavators they have, they will reach a similar nest size. However, in the 100 worker fragments, the nest area relies on how many excavators dig.

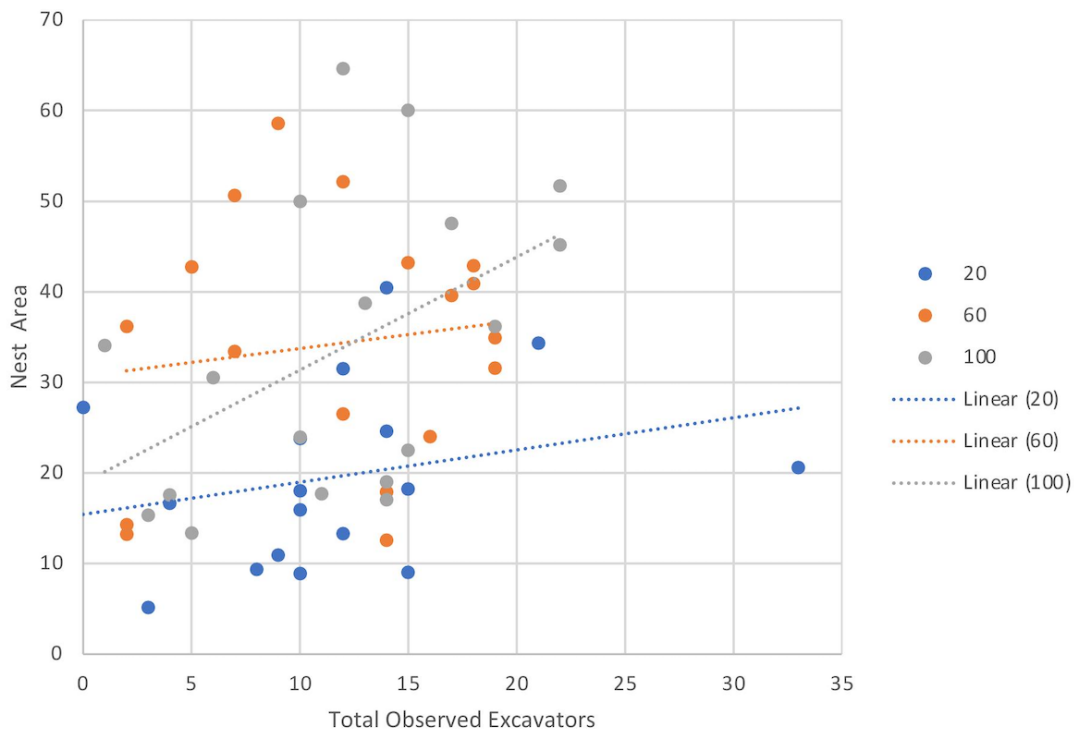


Figure 12 Shows the relationship between the observed individual excavators and the area of the nests.

Discussion

Individual task allocation and fidelity

We found that the proportion of effort changed throughout the five days of trial, but the proportion of excavators remained the same across the three treatments. We found that excavators and non-excavators switched between tasks equally. However, we saw that task fidelity was less common, we didn't observe a pattern where certain ants were observed doing the same task everyday. In contrast to the *Formica* ants which showed 98.6% task fidelity.^[2] That might be because they've been captive for up to a week. As a response to captivity, workers might have exhibited weaker task fidelity than they would in the field. In addition to that, the fact that we provided them with food and water (things they usually have to work for) might have also affected their task fidelity. It's important to note that these are very different species so it just might be that Harvester ants switch tasks more frequently than Formica ants.

In figure 5 we see that the number of excavators started to decline after day 2 which makes sense because fatigue or being put in this new stressful environment may contribute to less activity. Stress might be responsible for the increased rate of communication between individual workers. As a result of those interactions, we would observe individual ants devoting their efforts toward finding a way out of the experimental box. These observations match research done on *Pogonomyrmex barbatus* stating that workers receive cues or signals from other workers from antennal contact. This might influence the task that these ants take on next.^[11]

Another hypothesis explaining why ants didn't have as high task fidelity as expected could be that the colors we used to paint their abdomen and observe them were challenging and hindered their performance. The paint color might have distracted them or other workers from work. Maybe it was a certain smell or texture that wasn't comfortable to work in.

How different colony sizes affect nest architecture

A significant correlation between colony size and measurements of nest area and depth was detected. However, colony size didn't significantly impact the complexity of nests. We expected to see a linear proportional relationship between colony size and nest depth, area, and complexity. For example, the 20 ant colonies would have the smallest nests, the 60 ant colonies would be intermediate and the 100 ant colonies would have the largest nests. This is not the case, results show that colonies with 60 and 100 workers had similar nest area and complexity outcomes. Colonies of 20 and 100 ants had similar nest depth outcomes while the 60 ant colonies had the deepest nests. There might be a threshold proportion of space vs colony size below which nest dimensions increase with colony size. Beyond this threshold, there will be too many workers sharing the space, thereby reducing digging and soil removal.

To take the above measurements we had to take pictures of the nests. To do so we moved the boxes out of their spot and put them on a desk to get a full view of the nest. Nevertheless, that might have caused turbulence for the ants, as it caused the entrance to collapse once and they had to dig it again. When replicating this experiment I suggest handling the boxes carefully, aiming for small to no movement.

For most of the experimental boxes, nest construction wasn't observed until the end of the first day when the ants got used to their newly created environment. It's a wise idea to put the ants in their nests for one day before the trial starts. However, we couldn't do that since the food we provided was only enough for 5 days. This meant we couldn't put more food in without risking some escaping or damaging the nests.

One additional thing to note when replicating this experiment is making sure all the workers that were collected from the same field colony end up together in the lab colonies. Ants can recognize their nest mates from pheromones and cues emitted by their bodies like cuticular

hydrocarbons.^[12] Allowing them to be around each other can help reinforce group identity within the lab colony and ensure that any subtle differences between worker ants from different field colonies do not affect the results of the experiment. If they are not separated correctly, the ants can fight among themselves or kill each other and their nest-building efforts will be hindered. This step is also important to ensure that the lab colonies that we observe and build data on are as accurate as possible to the real colonies in the field. Since Harvester ants have big field colonies with multiple entrances, it sometimes can be hard to know exactly where the worker ants come from out in the field when doing collections. Especially since most of the visible ants were foraging for food from one entrance to another. We managed this issue by using by identifying one nest entrance of a specific field colony in Islander Park. We collected the ants from around the nest entrance and kept as many workers as possible from that colony in the same trial to reduce the chance of any mixing. We also kept all ants from the same colonies in separate plastic containers to prevent any interactions with one another if we were to conduct trials with ants from different colonies.

Do individual behavior shape group outcomes

We found that the smallest lab colonies' nests didn't depend on the number of excavators as much as the bigger lab colonies did. We extrapolated the data from figure 12 to see what the relationship would look like over time, and we saw the same results. These results suggest the existence of a relationship where individual behavior affects nest architecture (at least as observed in the 100 ant colonies). We observed that colonies with more complex nests are less likely to have escaping ants. This is because more workers are dedicating their effort to nest-building.

One of the limitations was that we worked on this project in the summer so we couldn't keep the climate controlled most of the time. When we were taking observations, we turned an air conditioner on, dropping the temperature in the room, which we observed made the ants less active. This is because it was a lower temperature than the one they're used to in the field. When replicating this experiment, we recommend maintaining a stable climate for more accurate observations. Since we know that climate does affect the activity of the ants, more research could be done to compare their performance in different climate conditions and record how that affects the nest structure. Future studies could also investigate individual behaviors more frequently (more than once/day) to see whether ants change their behavior consistently over time or whether there are other factors involved.

Conclusion

Now we understand a little bit more about the relationship between individual behavior and communal outcomes with regard to nest architecture. This opens the door for future studies and I recommend future researchers incorporate more variables into this experiment. One additional treatment might be adding seeds daily to each colony to see if they dig more complex nests to store food. Since they are harvester ants I believe it would be beneficial to observe how they store the seeds underground.

Another treatment example could be introducing a queen to the colony and recording whether that affects their nest-building behavior. Will the nests then be more complex to protect the queen? I want to test this because, during ant collection for trial 3, we captured a queen and introduced her to an experimental box with 60 worker ants. We tried to observe the worker ants' behavior, however, that colony's box was attacked by Argentine ants so we couldn't observe them excavating. However, we did observe that the Harvester ant workers fought very hard to protect the queen. They ended up digging a small tunnel for her to hide in so as not to be reached by the Argentine ants. This observation suggests that the presence of a queen does influence individual behavior in a way that warrants further exploration. Conducting another study testing different queen types to see if that affects the community and its behaviors differently would yield interesting outcomes.

That being said, we still know a lot about the behavior of Harvester Ants. We will continue to learn more about their behavior and other insects in general through future research. Overall, this project was an interesting study of how nest architecture and division of labor affect community development in the Harvester Ant species. I would like to conduct a follow-up project in the future. However this time, I want to be able to test different chemical compounds to see which ones affect the development of the community as a whole and the individual interactions.

Future studies could investigate the relationship between the population density of colonies and the number of workers who contribute to each chamber of the nest. This will help to minimize conflict within the colony. This study could also be expanded to look at how ant colonies function in different environments and how factors like climate can affect a colony. Is it always the case that in colder climates all species of ants aren't active or are there species that originally live in colder habitats and whether or not they have to adapt to their environment in order to survive. I would also like to conduct this experiment using another species of ants to see if the results would be similar. The optimal conditions for an ant colony to thrive are a warm, humid climate and abundant food resources. However, not all colonies thrive under these conditions. Some colonies thrive in dry climates with little rain while others adapt to swampy environments with constant humidity. Studying how different species adapt and survive under different conditions could help us to develop techniques for preserving these species in the future. By studying the interactions between the different species within the colony, we can better understand how the colony functions as a whole and come up with ways to help them thrive.

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